The last of them, which bears the furca, is also unsymmetrically developed. In correspondence with the relative sizes of the two halves of the furca, the left side of the segment in question is considerably broader than the right. The serration characteristic of the furca of this species terminates regularly on each side just above the lateral seta, but on the right side it commences, not as on the left immediately beneath the hinder margin of the last segment, but somewhat further back. This malformation may be original, but is more probably produced by a subsequent accident (perhaps in change of skin). In the reproduction of the lost part of the furca it was not again completed of the normal size; but in this way certainly the displacement of the above-mentioned seta is not easy to explain.

XL.—*Considerations on the Structure of Rhizopod Shells.* By Friedrich Dreyer *.

In the course of my investigations upon Rhizopoda, and especially upon the Radiolaria, various considerations of a general character have impressed themselves upon me. In part similar ideas have been already touched upon by previous authors and occur scattered in the most various parts of the copious literature; several points to be referred to in what follows I have already incorporated with the special investigations in the first part of my 'Radiolarienstudien' †; nevertheless I regard it as a not unprofitable task to reproduce in the following pages in a connected form the complete train of thought of my considerations upon the structure of the Rhizopod shells, as I hope that it will be of interest even for many who do not occupy themselves specially with the Protistan group in question.

Even on a superficial consideration of the enormous number of forms of the Rhizopoda we may recognize in them an essential difference in the general habit of the shell, and, in accordance therewith, distinguish two groups of forms. One

* Translated from the 'Biologisches Centralblatt,' Bd. ix. pp. 333–352 (1st August, 1889).

† F. Dreyer, 'Morphologische Radiolarienstudien,' Heft I. "Die Pylombildungen in vergleichend-anatomischer und entwicklungsgeschichtlicher Beziehung bei Radiolarien und Protisten überhaupt, nebst System und Beschreibung neuer und der bis jetzt bekannten pylomatischen Spumellarien" (Jena, 1889).

portion of the Rhizopoda possesses a shell which is perforated by numerous uniformly distributed pores or by several—at any rate more than two—pores, and shows in the majority of cases a spherical or polyaxonic fundamental form without any clearly marked elongated main axis. Another portion of the Rhizopoda shows a distinctly marked, usually elongated, main axis of the shell, at one or sometimes at both poles of which there is an aperture. This aperture is either the sole opening which exists in the shell, or when the wall of the shell is perforated it is distinguished from the pores of the shell by its greater size and frequently by marginal ornamentation and similar differences of various kinds. In accordance with the characters just mentioned we may distinguish two kinds of structure in Rhizopod shells in general, which may be suitably designated the perforate-polyaxonic and the pylomatic*-monaxonic form-types. The principal and characteristic point in these two types of form is the constitution of the shell-apertures, whether uniformly perforated or pylomatic. It is only in the second place that the proportions of the promorphological axes come into consideration; these are in most cases dependent upon the nature and distribution of the shell-apertures and correlated therewith, as is very natural, seeing that the latter on the whole agree with the distribution and direction of flow of the sarcode passing outwards. The Rhizopods belonging to the pylomatic type are, from the nature of the case, without exception, monaxonic—the pylom is placed at one pole of the principal axis. The Rhizopod shells of the perforate type are in general spherically homaxonic or polyaxonic; in many cases indeed even here an abbreviated or elongated principal axis is developed; but this never presents a pylom at its poles.

The more or less uniform perforation, in accordance with its indifferent character, exerts no persistent influence of importance upon the form of the shell, and there is consequently nothing further specially to be said upon the perforate type.

* In my 'Radiolarienstudien' I have proposed the name of "Pylom" for the principal orifice of the Rhizopod shell. I have there employed it in the first place for the orifices occurring in the Radiolarian skeleton, especially in order to avoid any confusion with the "osculum" (Häckel) of the central capsule of the Nassellaria and Phæodaria (Osculosa, Häckel). As hitherto no unitary designation exists for the principal orifice even of the Thalamophora, it may be desirable to embrace the structures in question in the Rhizopoda generally under the term "Pylom." Upon the comparative morphology of the pyloms and allied structures, which is interesting in many respects, see the detailed exposition in my 'Radiolarienstudien.'

It is otherwise, however, with the pylomatic type. Hand in hand with the development of a chief aperture or pylom a series of transformations and differentiations occur in the Rhizopod shell, and these become particularly interesting because they are independent of the material of which the shell is composed and are developed independently in the most different groups of the Radiolaria and Thalamophora. From this it follows that here we have to do with purely analogical structures, which, standing in correlation with the formation of the pylom, occur only in the Rhizopod shells which are distinguished by a principal orifice. It may therefore be profitable to go somewhat in detail into these peculiarities of the monaxonic-pylomatic type.

The most usual accompaniment of the formation of the pylom is an elongation of the shell in the direction of the principal axis—more rarely this axis is abridged. If the shell possesses radial skeletal elements, spines, &c., a corresponding influence makes itself felt even in these—they arrange themselves, following the direction of the principal axis, in such a manner that those of the oral half of the shell are directed towards its oral pole and those of the aboral half towards the aboral or apical pole. Generally this process of differentiation goes still further, inasmuch as on the equatorial parts of the shell no spines are developed, but they are confined to the two poles. Then is produced an elongated, elliptical, or oval shell, one pole of which is occupied by the principal aperture. Further, the two poles of the principal axis are distinguished by radial spines or other structures; at the oral pole these surround the pylom as radial marginal ornamentations of various kinds, while the opposite apical pole is furnished either with a tuft of spines or with some generally regularly grouped spines, or with a single strong apical spine. This development of the shell is extraordinarily diffused in the most different divisions of the Rhizopoda, and it may be regarded as characteristic of the monaxon-pylomatic type. Corresponding forms occur in *Difflugia*, *Euglypha*, *Quadrula*, *Campascus*, *Lagena*, in numerous polythalamous Thalamophora, and most generally diffused in the Nassellaria, pylomatic Spumellaria, Challengerida, Circoporida, Tuscarorida, Medusettida, and Castanellida.

Instead of the marginal spinosity the pylom is sometimes produced into a tube. In many a pylom occurs also at the aboral pole, so that the shell, perforated by a mouth at both poles of the principal axis, acquires an amphistomous character. All these morphological characters of the monaxon-pylomatic type are allied phenomena and stand in close correlation both with each other and with the formation of the pylom. This is easily explained by the fact that all depend upon the same physiological cause in the soft body secreting the shell. All the peculiarities of the monaxon-pylomatic type, including even the formation of the pylom, are to be referred to a uniaxial differentiation of the sarcode-body, which no longer emits its pseudopodia equally distributed on all sides, but for the most part, or even exclusively (imperforate forms), from one point, namely through the pylom; next to this principal effluent point the flow of sarcode is strongest at the opposite pole, and, indeed, sometimes, as in the amphistome Rhizopoda, it is equally strongly developed at both poles. By this orientation of the soft body in the direction of a primary axis its formative or secretory activity is no longer equally great in all directions, but localized in a corresponding manner, so that the two poles of the principal axis are distinguished in the way above indicated by radial appendages of various kinds from the more indifferent equatorial parts of the shell.

In a very great number of cases it is proved by observation that a strengthened main flow of sarcode takes its course through the pylom, quite apart from the imperforate Thalamophora and Radiolaria, in which, from the very nature of the case, the whole of the pseudopodia must pass through the pylom as the only aperture present. We may therefore without hesitation regard such an arrangement as a general rule, without requiring direct proof for every pylomatic Rhizopod shell. From analogy, *i. e.* supported by the numerous actually observed cases and the harmonious intimate relation of the different parts of an organism which no one can very well doubt, this assumption is justified.

It might perhaps be objected, however, that the pyloms of the Rhizopoda being traversed by a stronger flow of sarcode does not prove that the latter is also the *cause of the formation* of the apertures; on the contrary, the opposite causal nexus might exist and the sarcode cords principally issue there, because a more convenient course is offered to them. In answer to this objection it will suffice to indicate simply that the soft *protoplasmic body* is the *original thing*, and the *hard structure* a *secondary secretion* from it. The soft body forms the shell for itself in accordance with its wants, instead of arranging itself to suit the shell; the apertures of the shell of course serve for the passage of the pseudopodia outwards, the small pores for single ones, the great pylom-aperture for a larger number of pseudopodia.

In a number of pylomatic Rhizopoda the development of a primary axis is not the only thing, but their fundamental form undergoes further differentiations. In the first place a difference of the transverse axes makes itself felt in such a way that a long and a short transverse axis may be recognized, these being perpendicular to each other and to the principal axis. The result represents the fundamental form of the amphitect pyramid (Häckel); the forms belonging here are lenticularly flattened laterally, *i. e.* parallel to the primary axis. In such Rhizopod shells, moreover, the pylom is frequently no longer round, but drawn out in the form of a slit; any spines present at the aboral pole are generally orientated in the direction of the longer cross-axis; sometimes the periphery of the monaxon-lenticular shell is keeled. Such more or less distinctly amphitect-pyramidal promorphs occur in *Hyalosphenia*, *Quadrula*, *Difflugia*, *Euglypha*, *Gromia*, *Lagena* (*Fissurina*, Rss.), and *Lingulina*, in some pylomatic Spumellaria *, in various Nassellaria, and throughout in the Phæodarian family Challengerida.

A further step towards higher differentiation is the transition to the eudipleural (bilaterally symmetrical) fundamental form, which may start either from amphitect or from simply monaxonic forms. This takes place in general in consequence of an elongation of the pylom (which in monaxonic and amphitect Rhizopoda is situated at one pole of the primary axis, and, indeed, directly perpendicularly beneath the apical pole of the shell) forward or backward, by which means a front and back and right and left become distinguishable. It is interesting to mark the agreement of this process with the transformation of the primary form in the hypothetical development of the Turbellaria from Ctenophora (A. Lang). The Ctenophora and earliest Turbellaria are perfectly amphitect in structure; the mouth is placed in the middle of the underside perpendicularly beneath the apical pole of the body, front and back, right and left are not yet distinguishable, and this distinction is only produced by elongation of the mouth forward or backward, which occurs in most Turbellaria (Polyclada), and by which the eudipleural fundamental form is given. Moreover, many Rhizopoda become eudipleural by a corresponding arrangement of the oral and aboral radial appendicular structures or by a bending round of the apertural neck of the shell. Eudipleural development of the shell occurs in *Difflugia*, *Trinema*, *Cyphoderia*, *Campascus*, *Lieberkühnia*, *Microgromia*, *Platoum*, *Plectophrys*, and *Lecythium*, in many

* The pylomatic Discoidea and Larcoidea are, however, to be excepted from this series of phenomena. For further details upon this point see my 'Radiolarienstudien,' Heft i. pp. 98, 99.

polythalamous Thalamophora, some pylomatic Spumellaria *, and the Phæodarian families Challengerida, Medusettida, and Tuscarorida.

Close to the eudipleural forms come the spirally-wound Rhizopod shells, which are to be regarded essentially only as a continuation of the eudipleural ground-form by the process of terminal growth, which will presently be referred to more particularly. There are therefore, especially in freshwater Rhizopoda, very gradual transitions from simply eudipleural to spirally twisted shells. In this respect the *Difflugiæ* are particularly instructive, as in them all transitions from monaxonic to eudipleural and from these to spiral shells are represented; thus, for example, *Difflugia corona* is typically monaxonic, *D. marsupiformis*, with the pylom displaced forward, eudipleural, while, finally, *D. spiralis* already shows distinctly the half-turn of a spiral †. In the same way as in these first and perhaps still individually varying commencements in the freshwater Rhizopoda, the highly developed marine Thalamophora, often showing many spiral windings, have been developed, as is indicated, among other things, by the monaxonic central first chamber (the so-called embryonal chamber).

Having in the preceding submitted the Rhizopod shell to a short consideration with regard to its *form*, we may now proceed to examine it somewhat more closely from another point of view, namely as to the mode of its *growth*. In this, at the first glance, we meet with an interesting parallelism with the two form-types just referred to. Just as in the case of these form-types we can also distinguish in the mode of growth of the Rhizopod shell two principal types, which may be placed side by side with the two form-types, and on the whole are to be conceived as a continuation of the latter caused by growth. Thus the perforate form-type corresponds to the concentric type of growth, and the pylomatic form-type to the terminal type of growth.

The concentric growth-type, as implied by its name, consists in that the soft body during its further growth around its first spherical perforate shell, which gradually becomes too small for it, separates externally successive larger concentric spherical shells. The shells of such a system of latticed spheres nested one within the other are bound together

* The bilaterality indicated in a great number of Nassellaria by the relations of the basal and apical spines is original and does not belong to this category. See 'Radiolarienstudien,' Heft i. p. 100, note 2.

† See 'Radiolarienstudien,' Heft i. Taf. vi. figs. 88, 89, 90.

by radial rods, the so-called radial beams. The growth of the hollow spheres following upon the first shell in a great number of cases (perhaps always?) even proceeds from the radial beams, the ends of these, which radiate freely outwards as radial spines, emitting a system of lateral apophyses, which grow together and complete the next shell. This is the typical and original form of the concentric shell-growth; it occurs, like concentric growth in general, only in Radiolaria, and, indeed, in Sphæroidea, many Prunoidea, the Phacodiscida, and the Phractopeltida. This original course undergoes modifications by the growth taking place no longer on all sides, but instead of this in definite directions. Thus the disciform Discoidea grow only in one plane by the addition of concentric rings; many Prunoidea only in the direction of one axis, as in them a series of dome-shaped segments of spheres are added successively at the two poles. Both modifications, however, may be easily referred to a system of concentric spheres and explained naturally as follows:—That in the Discoidea only those parts of the latticed spheres which are situated in the plane of growth are developed as rings, while in the Prunoidea only the sphere-segments placed at the two poles of the principal axis in which growth takes place are developed.

As we have seen, in the concentric growth-type an addition of new portions of shell originally takes place uniformly in all directions, or in the last-mentioned modified modes of the phenomenon at least in more than one direction. In opposition to this the shells of the terminal growth-type grow only in one direction. Just as the concentric growth-type is associated with the perforate form-type, so is the terminal type of growth with the pylomatic form-type. Terminal shell-growth takes place in this manner:—The sarcode-body of a pylomatic shell, as soon as the latter becomes too small for it, swells forth in part from the pylom, and in front of this forms a second shell (here usually called a chamber or joint), which opens outwards by a new terminal pylom. In the further growth of the soft body this process is repeated again and again; in advance of the pylom of the second chamber a third chamber is formed, in front of this a fourth, and so on. In this way longer or shorter series of chambers are produced, which continue to grow at their extremity, the orificial pole of the youngest chamber. The series of chambers is either straight, as in Cystoidea and Nodosariæ, or curved, as in *Dentalina*, or rolled into a spiral (e. g. *Cristellaria*), like the shells of the Nautiloidea and Ammonites, only in the latter the soft body is exclusively in the last or youngest chamber, whereas in the Rhizopoda all the chambers are filled by the sarcode-body.

While the whole of the Rhizopod shells may be brought under the two form-types, this is not the case with the growth-types, for the simple reason that in many Rhizopoda no supplementary growth of the shell takes place. These are the one-shelled or single-chambered forms without secondary growth *, which are to be recognized in considerable numbers both in the perforate and the pylomatic types and both in Radiolaria and Thalamophora; these stand in a certain opposition to the shells with secondary further growth occurring in one or other of the two growth-types. It is interesting to see that, apparently, there is a physiological difference to be placed side by side with this morphological distinction. Verworn † has observed that artificial injuries to the shell of a monothalamous Rhizopod (*Difflugia urceolata*, Carter) were not repaired, while in the polythalamous Rhizopods this takes place to the fullest extent, as shown by that author's investigations upon *Polystomella crispa* and Carpenter's on *Orbitolites tenuissima* and *O. complanata*. From these results we may conclude with Verworn that the faculty of the soft body of secreting shell-material only continues as long as the normal growth of the shell itself, from which then the above-mentioned different behaviour of the mono- and polythalamous Rhizopoda may be explained.

As already mentioned, the two form- and growth-types are associated in this way:—the shells of the perforate type are further developed in accordance with the concentric growth-type, and the pylomatic shells, on the contrary, after the terminal growth-type. To this rule, so far as I know, only one exception is known, namely that of the Phæodarian family Canosphærida. The members of this interesting group possess a small, pylomatic-monaxonic, central shell, surrounded at a considerable distance by a large, spherical, homaxonic, latticed ball, the two shells being held together by long radial beams. Here, certainly, the sarcodic stream in one direction which existed at the time of the secretion of the central shell is suppressed during the course of the succeeding development, to give place to a uniformly radial arrangement.

* Even some monothalamous Thalamophora show a secondary shell-growth, such as, especially, the Cornuspirida. These pylomatic forms of course belong to the terminal growth-type, and are therefore to be excepted here.

† "Biologische Protistenstudien," in Zeitschr. f. wiss. Zool. Bd. xlvi. pp. 455–470, Taf. xxxii. Translated in 'Annals,' ser. 6, vol. ii. p. 155.

Having now briefly indicated the relation of the polythalamous to the monothalamous forms, the question naturally occurs to us which of the latter, the shells without secondary growth, are to be regarded as the most primitive. A careful investigation of the conditions coming under consideration shows us that a positive answer to this question cannot be given. The perforate, more or less homaxonic Monothalamia in almost all cases show a primitive character; but this may also be assumed with a very high degree of probability for many pylomatic Monothalamia. On the other hand, it is exceedingly probable that a great part of the pylomatic Monothalamia have only arisen secondarily from perforate spherical forms. This view is supported especially by some important transition-forms which occasionally occur. Thus the number of pores in the spherical shell of *Microcometes* varies from 5 to 1, so that in the latter case we have already the indication of a monaxon-pylomatic development; and in *Thurammina* and *Orbulina* one shell-pore is sometimes distinguished from the rest by its greater size. In Radiolaria the secondary origin of a pylom occurs very widely, and with regard to this I may refer to the detailed treatment of the point in my 'Radiolarienstudien.'

Whilst, therefore, one form-type may pass over into the other, this is by no means the case with the growth-types. It never happens that a form which has grown terminally for a time afterwards adopts the concentric growth, or the reverse. According to extant observations at least it may pass as an unexceptional rule that the same form always remains true to the growth-type which has once been adopted. The behaviour of the pylomatic Spumellaria is particularly instructive upon this point. Not only in many single-shelled Spumellaria, but also in many in which several concentric spherical or annular systems are already present, a pylom is developed; but nevertheless these forms continue without disturbance to grow concentrically, the influence of the pylom not being of sufficient importance to suppress the concentric growth and cause the shell to continue its growth terminally. The Rhizopoda in question are able to change their form-type, but not their growth-type.

In what has been said mention has several times been made of developmental or transformational processes in the Rhizopod skeleton; with regard to these the following must also be brought to mind. For the genetic explanation of the innumerable phenomena of differentiation three possibilities have been given in accordance with the different particular results. A great number of structures are referable to simple appositional growth; other changes, on the contrary, are only to be explained by the disappearance of previously existing parts of the skeleton; while, finally, certain alterations are intelligible only by flexion of the skeletal parts involved in them. If we now take into consideration that the hard parts of the Rhizopoda consist of rigid mineral material, it is clear that ontogenetic developmental processes are possible only in the first mentioned way by the addition of new material. It is true that a process of resorption has already been repeatedly assumed to take place in the shells of Thalamophora, and such a process might really be conceivable, perhaps by local production of acid by the soft body; but this appears so problematical that we cannot deal with this factor until its existence has, at least once, been demonstrated with certainty. In the case of the siliceous skeletons of the Radiolaria a process of resorption is to be rejected *à priori* upon easily intelligible grounds. So also, of course, a flexion of rigid calcareous and siliceous parts is impossible. Hence it appears that the ontogenetic development of the hard parts of the Rhizopoda can take place only by appositional growth, and all structures which cannot be explained thereby must be ascribed to phylogenetic development, as of course by means of phylogeny any conceivable alteration of form is possible.

The circumstance that in the case of the hard parts when once secreted, subsequent re-solution or alteration by total or local resorption, flexion, extension, and the like is no longer possible, involves another exceedingly important consequence. As in the higher Protista, in which already we may speak of a true individual development, and which therefore have their genealogy behind them, and to which, of course, the biogenetic fundamental law applies as to plants and animals, so also the ontogeny of the skeleton of the Rizopoda furnishes a more or less exact reproduction of their phylogeny. But while, in the higher organisms after the completion of the ontogeny, the individual stages passed through during the latter have generally long since disappeared, in the Rhizopod skeleton the entire development which has been passed through is still completely preserved in the adult specimen. In order to obtain an accurate picture of the development of the shell, it is only necessary to examine the earlier-formed parts back to the youngest, therefore in shells with concentric growth to pass from the centre to the periphery, and in those with terminal growth, from the so called embryonal chamber along the series of chambers to the end. Therefore, as in the known example of the Cephalopod shell, it is very often possible also in the Rhizopod shell to compare directly the initial parts of differentiated skeletons with adult primitive forms. With the shells of Thalamophora this has been carried out in several special cases; and in the case of the Radiolaria, from their much greater differentiation it is possible to a much greater extent and with more profit. In these cases comparative anatomy and ontogeny coincide, an advantage in morphological investigation which cannot be too highly appreciated, but which, unfortunately, like the comparative treatment of the Rhizopoda in general, has hitherto by no means received sufficient attention.

Having now become acquainted with some of the most important points in the structure of the shells of the Rhizopoda, it remains for us to give an explanation of these phenomena. Here, of course, we can only have to do with a preliminary attempt to throw some light upon the ætiology of the enormous form-labyrinth of the Rhizopoda, for even an approximately complete solution of this difficult problem still lies in the far distance.

The chief cause of the form-types of the soft body and of the shell is to be sought in the mode of life of the Rhizopoda under consideration. Rhizopoda with shells belonging to the perforate form-type and with pseudopodia radiating uniformly on all sides will live free and rotating in the water. The monaxonic and amphitect shells of the pylomatic form-type will belong to Rhizopoda which, in swimming or creeping, maintain a definite, perpendicular principal axis. The eudipleural development, lastly, owes its origin to creeping in a particular direction, just in the same way as in the example of the Polyclada already adduced in this connexion.

The morphological evolution or the specific character of the form-types recurs, as has already been mentioned, in exactly analogous development throughout, independently of conditions of relationship and shell-material. With regard to the perforate form-type, on account of its undifferentiated character, there is not much to be said in this respect; and here we have chiefly to consider the above-mentioned associated phenomena of the formation of the pylom, such as oral marginal ornaments of the pylom, apical spinosity, &c. The specific evolution of the form-type once selected is, as has been said, independent of the shell-material; in the selection of the form-type itself, however, the latter plays an important part, and this applies in a still higher degree to the growth-type, inasmuch as the structural material plays a positively determinant part with respect to the mode of growth of the Rhizopod shell.

The most important materials here coming under consideration as being employed by the Rhizopoda in the construction of their shell are of threefold nature*. A part of the Thalamophora construct their shells of agglutinated foreign bodies, partly inorganic (sand, mud), partly of organic nature (Thalamophoran and Radiolarian shells, sponge-spicules, &c.), while the greater part of the Thalamophoran shells are formed by secretion of carbonate of lime; and, thirdly, the skeletons of the Radiolaria consist of silica. The two first-mentioned materials of the Thalamophoran shells have this in common, that they possess far less firmness than the silicic acid of the Radiolaria. This distinction has also as its consequence a corresponding difference in the habit and mode of construction of the two great primary groups of the Rhizopoda.

Even upon a superficial examination one is struck with the fact that the shells of the Thalamophora with much less multiplicity of form and differentiation are far more massive and stouter than the Radiolarian skeletons, which are often exceedingly complicated, graceful, and elegant. The comparatively soft material which is employed by the Thalamophora in the construction of their shells does not permit these Rhizopoda without injuring the stability of their dwellings to make such airy and complicated structures as the Radiolarian skeletons, composed of solid more or less elastic siliceous rods.

The distinctions, however, are of a still more profound nature, and extend not only to the external habit, but also to the whole structural plan of the shells and skeletons. Even in the single-shelled forms, this, as already indicated, may be distinctly recognized in the selection or distribution of the form-types in the two great sister-groups of the Rhizopoda. The monothalamous Thalamophorous shells are almost all pylomatic, and only a few forms, such as *Orbulinella*, *Orbulina*, and some sandy-shelled forms, belong to the perforate form-type. On the other hand, among the Radiolaria the

* The primary chitinous shell of many freshwater Rhizopoda plays too subordinate a part in the matters here under consideration to need any special mention. The shell-material of the Phæodarian families Circoporida, Tuscarorida, and Challengerida requires closer investigation. It appears, however, to have a similar consistency to the calcareous material of the Thalamophoran shells, and the mode of construction of these Phæodaria is like that of the Thalamophora. Acanthin appears, with regard to its solidity, to hold a middle place between carbonate of lime and silicic acid, at least this holds with regard to the habit of the Acantharian skeletons, which, on the one hand, are more differentiated and elegant than the Thalamophoran shells, without, however, on the other, attaining the light construction and great complication of the siliceous skeletons of the Polycystina and Phæodaria.

majority of the single-shelled forms are perforate, and the pylomatic-monaxonic forms are in the minority, although they do not fall so far behind the others as does the perforate form-type among the monothalamous Thalamophora. This distinction in the distribution of the two growth-types becomes still more strongly marked, however, in the many-shelled forms with secondary growth. Thus in the Radiolaria both growth-types occur widely distributed side by side, but still in such a manner that a preponderance of the concentric growth is unmistakable, while, on the contrary, in the Thalamophora the terminal growth-type is exclusively * represented.

The cause of this different behaviour of the Thalamophora and Radiolaria is to be found in the fact that the two modes of construction in question make different demands upon the solidity of the material. The perforate-concentric shell-construction requires much finer material than the pylomatic-terminal, and therefore it happens that, while in the siliceous skeletons of the Radiolaria both shell-constructions are represented in the highest completeness and complication, the Thalamophora are under the necessity of producing exclusively pylomatic-terminal shells, for with their material of construction, which is softer in comparison with silica, it would not be possible for them without impairing the solidity of their shells to form concentric and airy skeletons like those of the Radiolaria; they must make their shells thicker and more massive in order to give them the necessary solidity.

It is in the essence of the perforate-concentric mode of construction that it requires to be carried out more lightly. As there is no principal orifice, the passage of the sarcode to the outer world, and in many shell-forms also between the different interspaces of the shell, is consigned exclusively to the pores of the shell, which for the purpose of ready communication must not be too narrow nor the intervening skeletal parts too massive; further, the union of the latticed spheres concentrically nested one within the other is only possible by means of free radial rods, which, again, must not exceed a certain thickness. The conditions of the pylomatic-terminal mode of construction are very different. Here the

* Only one remarkable exception to this rule is furnished by *Thurammina papillata*, Brady, the agglutinated shell of which is composed of two concentric spherical shells united to each other by some radial beams (Brady, 'Challenger' Report, pl. xxxvi. fig. 12). The stout and rather irregular character of this form shows us, however, that we have here to do as it were only with an unsuccessful attempt to imitate the light construction of the siliceous skeleton with a less solid material.

pores pass much into the background, both in importance and development, in the presence of the principal orifice, the pylom; in the Imperforata they are even entirely wanting, and the shell-wall can therefore be made more compact and solid. Further a union of the different shells in polythalamous forms by means of free radial beams is unnecessary, but they lie with their walls directly upon each other. In the pylomatic siliceous shells of the Nassellaria the pores certainly are not inferior in their development to those of the perforate-concentric Spumellaria, but this is simply because the silica of the skeletons of itself gives them such firmness that by it a strengthening of the shell-wall and the consequent reduction of the pylomatic form-type is rendered superfluous. It is otherwise with the shells of the Challengerida, Medusettida, and Tuscarorida, which are indeed of siliceous nature, although not of homogeneous consistency, but possess a more or less complicated internal structure, or consist of a mass of separate siliceous spicules cemented to each other. The forms belonging here therefore show distinctly a recurrence of perforation, while the wall is at the same time thick.

The character of the Spongopylida, spongy Discoidea in which a pylom has been formed secondarily at the margin of the disk, and which I have united under this character in the genus *Spongopyle*, is exceedingly instructive, and in fact demonstrative of the conception of these conditions here developed. Thus *Spongopyle aspera*, which consists of an irregular tangle of thin siliceous rods, shows, as indicated by its name, a rough irregular surface; in *Spongopyle osculosa*, *S. setosa*, *S. craticulata*, and *S. Stöhrii* a more uniform external closure is perceptible; and this process finally attains its highest point in *Spongopyle circularis*, *S. ovata*, *S. elliptica*, and *S. variabilis*. In these forms the spongy tissue of the interior is shut off externally by a continuous shell, in which there are only some very small pores. At the margin of the disk is placed the pylom as a single larger orifice. By the development of this as the principal opening for the outflow of the sarcode a compact closure of the other parts of the spongy disk has been rendered possible, and this again, by the external fixing of the spongy skeletal web, and by giving protection against injurious external attacks, is of service. The phylogenetic development of an external shell-mantle indicated by the comparative anatomy of the species of *Spongopyle* is completed and confirmed by my observations upon the ontogeny of *Spongopyle osculosa*. The young stages of this species possess a rough surface open on all sides, and an external, continuous shell-closure is developed only after the completion of the growth of the spongy disk *.

As we have seen, the agglutinated and calcareous materials agree in that, as compared with the silica, they possess less firmness, the consequence of which is that the Thalamophoran shells are more compactly and simply constructed than the siliceous skeletons of the Radiolaria. On closer examination, however, a distinction may be recognized between the agglutinating and calcareous Thalamophora, consisting in the fact that the former are more coarsely and simply constructed than the latter, and this is certainly due to the agglutinated constructive material being inferior in solidity to the homogeneous calcareous mass. Although this difference is not so great as that between Thalamophoran and Radiolarian shells, it nevertheless exists, and to all appearance its importance must not be undervalued. Quite recently Neumayr has specially called attention to this circumstance, and made use of it for a phylogeny of the Thalamophora, assuming the more highly differentiated calcareous-shelled forms to have become developed from the simple arenaceous-shelled types as their stem-forms †. It will be most convenient, in the first place, to reproduce this theory of Neumayr's in the author's own words. He says :—"The low forms furnished with the most imperfect shell-structure which form Brady's very well-founded family Astrorhizidæ are exclusively sandy ; the most highly developed Foraminifera, furnished with a branched canal-system, double septa, an intermediate skeleton, &c., are exclusively calcareous ; while the forms standing between the two are partly sandy, partly calcareous, and show many transitions from one development to the other. This condition of things leads to the supposition that arenaceous forms, without any trace of a complicated structure, such as we find in the Astrorhizidæ, represent the stem-types from which the other Foraminifera have been developed. . . . In favour of the notion that the arenaceous Foraminifera in reality represent the original type, we have in the first place their geological occurrence, inasmuch as they occur in old deposits in comparatively much greater number than subsequently ; it is true that in the comparison of the living with the Tertiary and Mesozoic species this does not appear so strikingly, but it is perfectly distinct

* See for further details my 'Pylombildungen,' Abschnitt v. Taf. v. figs. 64–69, and Taf. vi. figs. 97–100.

† Neumayr, "Die natürlichen Verwandschaftsverhältnisse der schalentragenden Foraminiferen," in Sitzungsb. Wien. Acad. Bd. xcv. Abth. 1 (1887), and also in 'Die Stämme des Thierreichs,' Bd. i (1889).

when we turn to the Palæozoic formations, and especially the Carboniferous, which here alone has furnished a rich Foraminiferan fauna. . . . In another phenomenon we find a further confirmation of the opinion that the calcareous Foraminifera have been developed from the arenaceous forms. It has already been mentioned that in both divisions there often occur parallel forms which show a great similarity to one another in their whole conformation ; but on closer examination, at least in a number of groups, the circumstance that the differentiation and individuality of the different types are much less in the arenaceous than in the calcareous series becomes exceedingly striking . . . Moreover, when we can trace the same types in the two divisions the characters appear much more distinctly and clearly in the calcareous forms; although transitions are present, the different types do not melt into each other so completely as in the arenaceous forms, and the multiplicity is much greater than in the latter." (Stämme des Thierreichs, pp. 168–169.)

This most recent conception of the natural system or phylogeny of the Thalamophora is decidedly to be characterized as a very happy idea, and deserves to be greatly preferred to the various attempts previously made at a natural grouping of the Thalamophora. A special advantage of Neumayr's theory is to be found in the fact that it does not lay the principal stress upon any single character selected more or less arbitrarily, such as the perforate or imperforate constitution of the shell, the shell-material, or the number and arrangement of the chambers, which fault, as the author justly points out, affects all previously established so-called natural arrangements of the Thalamophora ; but it takes equally into account all the conditions which come under consideration. In this way we get a phylogeny which agrees better with both the morphological and the palæontological facts than is the case with the older systems. In accordance therewith the Thalamophora are divided up into a great number of more definitely limited groups, which, on the whole, agree with those established by Brady. These are distributed upon a small number (four) of great stems, which run parallel and independently side by side, and are connected only at the root by the primitive agglutinating Astrorhizidæ, the common stock-form of all the four stems. On the irregularly agglutinant Astrorhizidæ follow the regularly agglutinant forms, the simplest of which directly approach the common stock-group, while the more highly developed forms already take on a divergent direction and become distributed over the four main-stems established by Neumayr ; with them corresponding isomorphous calcareous forms are directly connected, while the most highly developed and most differentiated terminal types of the stems are exclusively of calcareous nature.

This phylogeny of the Thalamophora of Neumayr's harmonizes perfectly with our conception of the significance of the structural material of the Rhizopod shell, and the two theories lend each other a support which must not be undervalued. The lower and lowest forms find the coarse agglutinated material quite sufficient for the construction of their simpler shells; the forms of medium complication already for the most part have recourse to carbonate of lime; while, finally, the most differentiated types construct their shells exclusively of lime, because this finer and firmer material alone renders possible that complicated structure which could not be carried out with the coarse and less solid agglutinated material. Only in the case of one of Neumayr's assumptions I should consider a certain limitation necessary. As appears from the last of the passages above cited, Neumayr regards the more imperfect and coarser construction of the arenaceous forms in comparison with the isomorphous calcareous ones as a primitive condition, and a special proof that the arenaceous forms are to be regarded as forerunners of the calcareous. In most instances, in all probability, this is the case, but not without exception. It is possible, nay, highly probable, that, as at the present day, the shell-material varies in certain forms with changes of the external conditions under which the Rhizopoda in question live; this has also occurred now and again during the phylogenetic development, and calcareous forms may thus be compelled to make their shells of sand. These will then, in consequence of the coarser material, appear ruder and less differentiated than the calcareous stem-form. Although the sarcode-body of such forms will have inherited the tendency to secrete hard parts equally well-developed morphologically, it will be unable, on account of the coarser nature of the sandy material, to bring this faculty to full development, as was the case with the calcareous material. Just as the Thalamophora in the course of their phylogenetic development were compelled, for the purpose of the higher morphological development of their shells, to pass, independently in the different stems, from the agglutinated material, which no longer sufficed for this purpose, to carbonate of lime, a form which is under the necessity of going back from the calcareous to the arenaceous development will also show a corresponding retrogression in respect of morphology. Such a change of material, as also the existence of isomorphous arenaceous and calcareous forms, occurs, however, only in Thalamophora moderately high in development, and, indeed, is possible only in them because here the corresponding morphological change extends only to unimportant peculiarities, but impossible in the highest and most differentiated types, such as the Nummulites for example, in which a reversion to the arenaceous grade of development would need to be accompanied by a profound change in the whole structure of the shell.

Thus, then, we have seen that in the three principal materials which come under consideration in connexion with the hard structures of the Rhizopoda, so many degrees of firmness and fineness may be recognized, which exert a very considerable influence upon the structure of the shells and skeletons. If we would illustrate these conditions by an example out of everyday life, we may fairly compare the agglutinated arenaceous material, the carbonate of lime, and the silicic acid, as the materials of the Rhizopod shells, on the one hand, with mud, stone, and iron, the three most important substances in the buildings made by man. The mud-structures, like the arenaceous Rhizopod-shells, can be carried out only in a rough and more or less primitive manner, like the birds' nests (such as those of the Swallows) built of mud, owing to the coarse texture and want of solidity in the material employed; in fact, the mutually adherent chambers of many "Agglutinantia" among the Rhizopoda possess a remarkable resemblance to the Swallows' nests aggregated together on the wall of a house. Stone-buildings and the calcareous Rhizopod shells take an intermediate position; while the siliceous skeletons of the Radiolaria and the infinitely varied iron structures of everyday life, from the great solidity of the materials, give the greatest room for complication and differentiation, and at the same time for multiplicity of form. It is not only the inherited faculty of the soft body to construct more or less complicated and differentiated skeletal parts that regulates the shell-structure, but, like human architects, the Rhizopoda are also more or less dependent upon their material, and must deal with its peculiarities.

As we have already seen, the concentric growth makes greater demands than the terminal upon the firmness of the material, and it is therefore met with only in the siliceous Radiolarian skeletons, while it does not occur among the Thalamophora. But at the same time the concentric skeletal structure has an advantage of which the terminal is destitute. A system of several nested spherical shells or parts of such shells forms an externally closed rounded whole which presents the smallest possible surface to external mechanical attacks; it is just otherwise with the products of the terminal growth-process, in which the different chambers are arranged one after the other in the form of a longer or shorter chain. Leaving out of consideration that such a series of chambers of considerable length is very obstructive to locomotion, it is comparatively very frangible, and from the statical or mechanical point of view disadvantageous. The Thalamophora avoid these disadvantages of the terminal growth and combine the advantages of the concentric shell-system with the terminal growth by generally not leaving their series of chambers in an extended state, but rolling them up spirally in the majority of the forms. As a further carrying out of the spiral convolution we must regard the reciprocal embracing of the chambers which occurs in a more or less marked manner in many Thalamophora. This embracing process occurs particularly typically in the Miliolida, and, indeed, we may here recognize a gradual increase from *Cornuspira* and *Spiroloculina*, in which all the whorls lie freely exposed, through *Quinqueloculina*, *Triloculina*, and *Biloculina* to *Uniloculina*. In the last-mentioned genus the process has attained its highest point, for here only the youngest chamber is freely exposed externally, while all the preceding chambers are completely enclosed by it. Here consequently exactly the same final result is attained as in the concentrically formed shell-systems of the Radiolaria, although in a quite different way. If the embracing of the chambers takes place only in one plane, this leads to the so-called cyclical growth, such as occurs in *Orbiculina*, *Orbitolites*, *Cycloclypeus*, and similar forms. There is thus produced within the terminal growth-type an apparently concentric growth, just as a number of discoid Radiolaria appear to grow spirally, that is terminally. These apparent exceptions to the rule above established, that no Rhizopod shell can change its growth-type, always turn out, however, on closer examination to be secondary convergences or analogical structures, although certainly sometimes deceptive *. In the same way that the Thalamophoran shells produced by general embracing may be compared with the concentric sphere-systems of the Radiolaria, the cyclical Thalamophoran shells represent the concentric ring-systems of the Discoid Radiolaria.

In conclusion may be mentioned the extremely interesting and significant fact that, according to the investigations of Naumann and v. Möller, Molluscan and Thalamophoran shells

* See 'Pylombildungen,' pp. 112, 113, and p. 101, note 1.

follow the same laws of circumvolution. From this it follows quite definitely that the spiral convolution which occurs in the same specific manner independently in two quite different groups of organisms having absolutely nothing to do with each other is not founded in the nature of the organisms in question, but has its cause in the circumstance of the external world, and is dependent on statical and mechanical requirements. We have a perfectly analogous case in the statically and mechanically adaptive structure of the " substantia spongiosa " of the bones of Vertebrates; and a series of my own observations make me regard it as very probable that the siliceous rods of a number of spongy Radiolaria are not arranged irregularly, as would appear to be the case at the first glance, but, in part, in accordance with definite laws. The next question which forces itself upon us in considering these results is whether this adaptive structure of animal skeletons has been produced by functional (Roux) or selective (Darwin, Weismann) adaptation. A discussion of the arguments which may be adduced for and against these two possibilities would, however, lead us too far, and pass beyond the bounds of these observations, especially as, without noticing it, we have got upon the question, at present so much in dispute, of the heritability of acquired peculiarities. The primary object of the preceding observations was more particularly to indicate the great fertility of a comparative treatment of the enormous abundance of forms of the Protista. The elegant and manifold hard structures of the Rhizopoda, which here particularly come under consideration, are by no means, as is sometimes supposed, mere *lusus naturæ*, but even they follow definite laws of structure. Only when we have advanced further in the recognition of the latter by means of more detailed investigations will the morphology of the Protista no longer be regarded (as is at present unfortunately often the case) as a mere playground of unscientific species-making, but will take its place as of equal importance by the side of the physiology of the unicellular organisms, which is much more cultivated and developed.